

OROBANCHE RIPARIA (OROBANCHACEAE),
A NEW SPECIES FROM THE AMERICAN MIDWEST

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ABSTRACT

Orobanche ludoviciana, with a range primarily in the Great Plains, is the most widely distributed species in sect. *Nothaphyllon*. It was first described by Thomas Nuttall in 1818 from a specimen collected at Ft. Mandan, North Dakota. During the following century and a half, most botanists had limited field experience with living plants of the genus and very few herbarium specimens with which to compare newly collected materials. This resulted in considerable confusion about the circumscription of this species and its geographic distribution. The treatments of Section *Nothaphyllon* (sect. *Myzorrhiza*) by Beck (1890, 1930) and Munz (1930) have led botanists to apply the species name too broadly to plants whose morphology was discordant with Nuttall's original protologue, and the problem of an overly broad species concept continues to linger. Earlier studies by the senior author led him to suggest taxonomic changes within the *O. ludoviciana* complex (Collins 1973) to address this problem, including formal recognition of two ecological races within *O. ludoviciana* sensu stricto with different host ranges: one inhabiting uplands and the other confined to bottomlands associated with major river systems. Recent additional investigations have revealed further evidence supporting recognition of these two races as distinct taxonomic entities. The present paper therefore discusses the morphological distinctions between them; it proposes retention of the upland form as *O. ludoviciana* and recognition the bottomland form as a distinct species, ***O. riparia***, sp. nov.

RESUMEN

Orobanche ludoviciana, cuya extensión abarca mayormente la zona de Great Plains, es la especie de mayor distribución en la Sección *Nothaphyllon*. El primero que hizo una descripción fue Thomas Nuttall en 1818, que se basó en una muestra recogida en Ft. Mandan, Dakota del Norte. Durante el siglo siguiente la mayoría de los botánicos tenían poca experiencia con plantas vivas de ese género y con ejemplares de herbario con las que comparar los materiales obtenidos. Por consiguiente hubo bastante confusión en torno a la circunscripción de esta especie y su distribución geográfica. Los estudios relacionados con la Sección *Nothaphyllon* (sec. *Myzorrhiza*) hechos por Beck (1890, 1930) y Munz (1930) hacen que los botánicos apliquen de modo demasiado amplio los nombres de las plantas cuya morfología es discordante con el protólogo original de Nuttall. El problema que permanece es el de un concepto demasiado amplio de la especie. Estudios doctorales conducidos por el autor principal durante los primeros años de la década de los setenta resultaron en cierto número de cambios taxonómicos sugeridos en el complejo *O. ludoviciana* (Collins 1973), incluso un reconocimiento formal de dos razas ecológicas dentro de *O. ludoviciana* sensu stricto con distribución algo diferente de los huéspedes. Una de las plantas era de tierras altas y es retenida aquí como *O. ludoviciana* y la otra confinada a tierras bajas asociadas principalmente con sistemas mayores fluviales y reconocida aquí como entidad sin descripción. Recientemente han salido a la luz más datos que apoyan dicha propuesta. En el presente trabajo se comentan las diferencias morfológicas entre estos dos ecotipos y se propone reconocer las poblaciones de las tierras bajas como una especie distinta ***O. riparia***, sp. nov.

KEY WORDS: *Orobanche*, Orobanchaceae, parasitic plants, broomrape, Flora of North America

Orobanche L. sect. *Nothaphyllon* (A. Gray) Heckard (sect. *Myzorrhiza* Phil.) comprises of an array of ca. 13 species that account for most of the taxonomic diversity within New World holoparasitic Orobanchaceae. It has been considered a monophyletic group by most botanists based on morphological and molecular data (Olmstead et al. 2001; Schneeweiss et al 2004; Bennett & Matthews 2006). Within sect. *Nothaphyllon*, two

major clades exist whose relationships have not yet been fully resolved: the *O. californica* Cham. & Schlttdl. complex (Heckard 1973), which has diversified mainly in the far-western United States; and the *O. ludoviciana* Nutt. complex (Collins 1973), which is widespread in the remainder of the United States and Canada, and southward into Mexico (also disjunct in southern South America).

Orobanche ludoviciana Nutt., with a range primarily in the Great Plains, is the most widely distributed species in sect. *Nothaphyllon*. It was first described by Thomas Nuttall in 1818 from a specimen collected at Ft. Mandan, North Dakota. Because most botanists during the following century had limited field experience with living plants of the genus and had very few herbarium specimens with which to compare newly collected materials, the species name was applied too broadly to include plants whose morphology is discordant with Nuttall's original protologue. The result has been considerable confusion about the circumscription of this species and its geographic distribution. All those who have treated Section *Nothaphyllon* (sect. *Myzorrhiza*) (Beck 1890, 1930; Munz 1930; Collins 1973; Heckard 1973), have at times recognized various infraspecific taxa, some of which are no longer accepted and therefore excluded from this discussion. Nevertheless, the lingering problem has been that of an overly broad species concept. Even Philip Munz (1930), who provided good insights into taxonomic variation within *O. ludoviciana* in his otherwise excellent taxonomic revision of sect. *Myzorrhiza*, overlooked significant morphological variation. Subsequent authors of floristic works who relied on his revision to determine specimens continued to some degree to overlook the taxonomic heterogeneity of plants treated by him as *O. ludoviciana* var. *genuina* Beck.

Doctoral studies by the senior author led him to suggest a number of taxonomic changes within the *O. ludoviciana* complex (Collins 1973), one of which was formal recognition of two ecological races within *O. ludoviciana* sensu stricto with differing host preferences: one inhabiting only uplands and the other confined to bottomlands associated with major river systems. Recent discoveries of new populations and examination of additional existing herbarium specimens of the bottomland plants have added evidence in support of this proposal. The present paper therefore discusses the morphological distinctions between these two ecotypes, and we propose to retain the upland form as *O. ludoviciana* and to recognize the bottomland form as a distinct species, *O. riparia*. It should be noted that, based on Collins's dissertation, the epithet *O. riparia* was discussed far in advance of the present publication by Musselman (1982, on Orobanchaceae in Virginia) and by Kartesz (1994, in a North American plant checklist), but neither of these usages affects the validity of the present description.

Bringing this new taxon to the botanical literature requires a brief review of the existing nomenclature and morphology of *O. ludoviciana* sensu stricto (*O. ludoviciana* var. *genuina*, sensu Beck). Several species of *Orobanche* in North America are commonly misidentified as *O. ludoviciana*, but are currently recognized as distinct species. They include *O. multiflora* Nutt., *O. cooperi* (A. Gray) A. Heller, *O. multicaulis* Brandegee, and *O. valida* Jepson. Of these, the two with the most morphological similarity and name association are *O. ludoviciana* and *O. cooperi*, and must therefore be contrasted with *O. riparia*.

Collins (1973) found that Munz's 1930 description and illustration of the corolla lobes of *O. ludoviciana* did not match the morphology of Nuttall's type specimen. The corolla lobes of the type specimen are rounded on both the upper and lower lips, but Munz's illustration, based on a specimen from White County, Illinois, shows a corolla with triangular-pointed lobes. Because Munz used material that matched his illustration in assembling his description of *O. ludoviciana*, subsequent regional and state floras continued to overlook the morphological heterogeneity between populations attributed to that species.

Repeated and extensive examination of specimens of *O. ludoviciana* sensu stricto from its entire geographic range has revealed that the character of rounded corolla lobes is consistent throughout for upland plants (Fig. 1). In contrast, the corolla lobes of bottomland plants, hereafter referred to as *O. riparia*, are consistently triangular and pointed (Fig. 1). The populations of *O. riparia* share several additional characteristics (Table 1): 1) They are found almost exclusively in river bank and sandbar habitats in floodplains; 2) The native hosts are annual members of Asteraceae tribe Heliantheae, subtribe Ambrosiinae, primarily *Ambrosia trifida* L. and *Xanthium strumarium* L., and occasionally *Ambrosia artemisiifolia* L. and *Dicoria canescens* A. Gray 3)

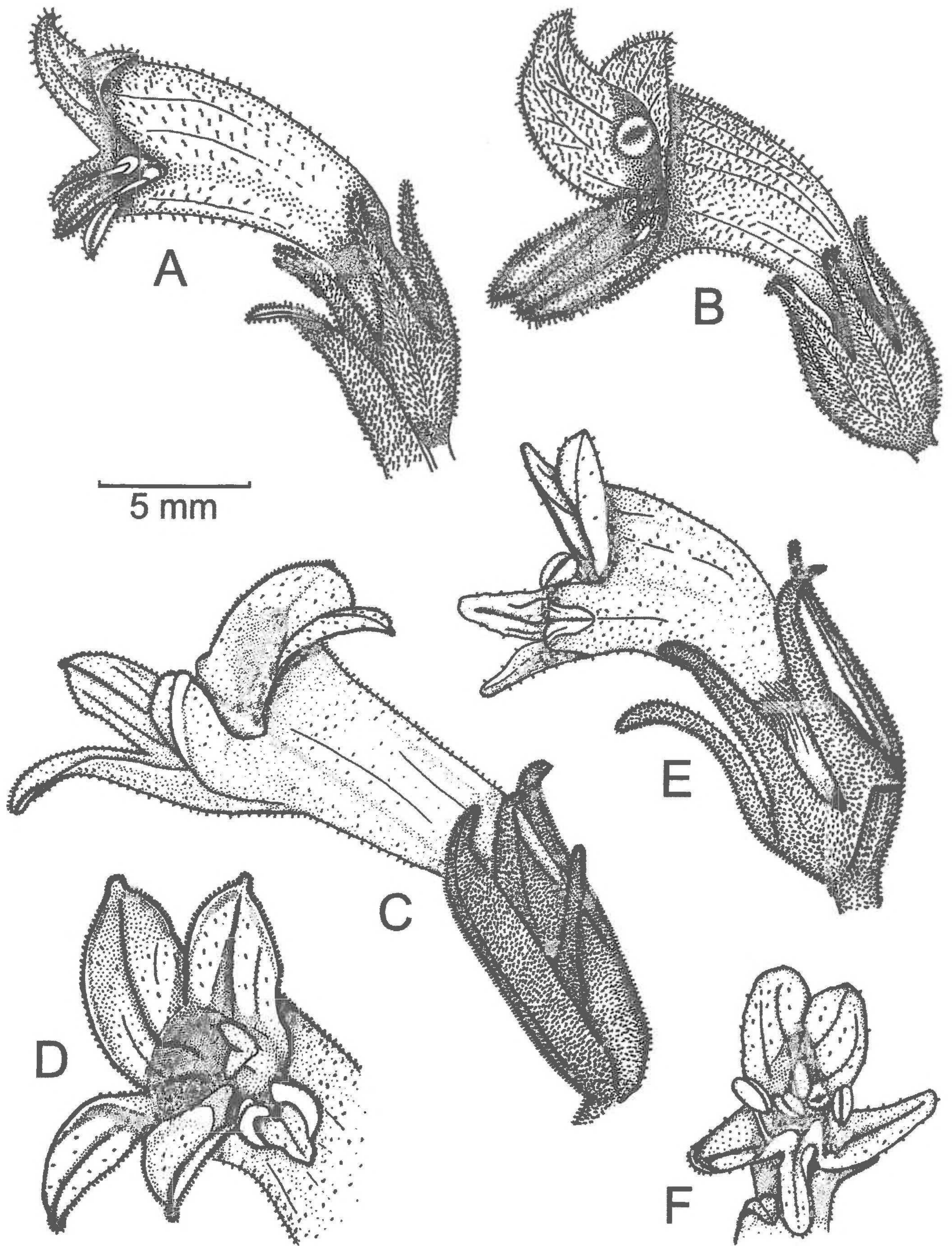


FIG. 1. Comparative illustrations of corollas of three species of *Orobanche*. A, B) *O. riparia*; A) eastern form, B) western form. C, D) *O. cooperi*. E, F) *O. ludoviciana*.

TABLE 1. Comparison of selected characters of three species of *Orobanche*: *riparia*, *ludoviciana*, and *cooperi*.

Character	<i>Orobanche riparia</i>	<i>Orobanche ludoviciana</i>	<i>Orobanche cooperi</i>
Calyx length	7–11 mm	8–14 mm	7–12 mm
Corolla length	15–22 mm	14–20 mm	15–32 mm
Shape and size of corolla lips/lobes	Triangular-acute, 4–5mm, erect or slightly reflexed	Rounded-obtuse, 4–8mm, erect or ascending	Triangular-acute, 5–8 mm, apiculate apex, ascending or reflexed
Corolla tube	Strongly curved, tube horizontal slightly flared distally	Slightly curved, tube ascending, slightly flared distally	Strongly curved, tube ascending, flared distally
Corolla color	Pallid, or upper lobe apex purple/lavender	Purple, lavender, rose, or pallid, tube exterior whitish	Dark purple on distal half with white exterior and throat
Pubescence	pubescent with glandular and eglandular trichomes or glabrate	Pubescent with glandular trichomes except inner lobe surface	Pubescent with glandular trichomes on tube, eglandular on inner surface of lobes
Flowering	August–October	April–August	December–April
Inflorescence arrangement	Open raceme, flowers in loose, regular spiral on floral axis	Compact raceme, flowers in dense, often irregular spiral on floral axis	Open or compact raceme with flowers in loose, regular spiral on floral axis
Primary hosts	Annuals; <i>Ambrosia</i> , <i>Xanthium</i> , <i>Dicoria</i>	Perennials; <i>Grindelia</i> , <i>Artemisia</i> , <i>Heterotheca</i>	Perennials; <i>Ambrosia</i>
Habitat and main range	River banks, sandbars eastern U.S. and prairie provinces	Prairie, desert, dunes; central and western U.S.	Sonoran Desert, ravines, dry stream beds, dunes; southwestern U.S.

The flowering period is from mid-August to early October; 4) Inflorescence color is typically pallid with only the interior tips of the corolla lobes tinted purple; 5) The corolla tube is strongly curved with the distal portion of the tube horizontal, slightly flared distally, and palatal folds that are either glabrous or densely pubescent.

Compared with *O. riparia*, *O. ludoviciana* has slightly shorter corollas with a flared throat and rounded corolla lobes (Table 1). It occurs mainly through the Great Plains (and eastward along the Prairie Peninsula) in various habitats, including sandy prairies, sand dunes, dry washes, calcareous (caliche) soils, and lower slopes of the Rocky Mountains. Its hosts are almost exclusively perennial members of Asteraceae tribes Astereae and Anthemideae, including *Grindelia squarrosa* (Pursh) Dunal, *Heterotheca* spp., *Artemisia* spp., and occasionally other genera. The principal flowering period is from late April in the southern plains through mid-August in the northern plains, although sporadic flowering has been observed rarely at other times in marginal habitats. The corolla tube is slightly curved at the constriction, ascending, and flared distally, with the palatal folds sparsely pubescent. Floral pigmentation varies from purple to pale rose and occasionally yellow, usually with dark purple upper lobes (Table 1).

Additionally, populations of *O. riparia* are ecologically and somewhat geographically distinct, and the habitat distinction is maintained in the western populations, where the two ecological races are geographically somewhat sympatric. Populations east of the Mississippi River (but including Missouri) are allopatric with *O. ludoviciana*. West of the Mississippi River, sympatry of the two species occurs from eastern Nebraska and Kansas to eastern Colorado, southward into New Mexico and the Texas Panhandle. A small overlap in flowering times in early August could provide an opportunity for hybridization between the two species. Although no suspected cases of hybridization have been observed based on morphology or field observations of populations, more definitive data from genetic studies are needed to answer this question. Molecular studies by Colwell are currently underway.

Munz (1930) treated *O. cooperi* as a variety of *O. ludoviciana*, but subsequent authors mostly have accepted it as a separate, but closely related species (Shreve & Wiggins 1964; Munz 1974). *Orobanche cooperi* is

distinguished by its dark purple color, larger, ascending corolla tube, and erect or strongly reflexed, triangular lobes with apiculate apices. The corolla tube has a white exterior and is slightly curved and flared distally, with palatal folds pubescent at the mouth and becoming glabrous in the throat. The habitat is primarily Sonoran Desert scrub, often associated with washes that remain dry except in monsoon season. Its hosts are shrubs in various tribes of Asteraceae, principally species of *Ambrosia* and *Encelia* (all Heliantheae, Ambrosiinae), but also reported on *Gutierrezia* (Astereae). The flowering period is mainly December through April (Table 1). Collins (1973) found that the cross-sectional stem anatomy of *O. cooperi* and *O. riparia* are very similar and that *O. ludoviciana* differs significantly from both of the other taxa.

Several characters suggest that *O. riparia* is more closely related to *O. cooperi* than to *O. ludoviciana*. *Orobanche riparia* and *O. cooperi* share an affinity for riparian or water-eroded habitats and hosts in the subtribe Ambrosiinae. They differ in that *O. cooperi* occurs only in seasonally arid habitats, whereas *O. riparia* occurs in both mesic and semi-arid habitats, and that the former parasitizes shrubby hosts, whereas the host taxa of the latter are annuals. The pubescence of the corolla lobes in both species is eglandular on the inner surface with vestiture considerably longer than the short glandular trichomes typical of the exterior surface. Likewise, the palatal folds are invested with eglandular trichomes, differing between the species only in their distribution on the folds. This shared pattern of trichomes is more evident in the western populations of *O. riparia* than in the eastern populations. Similarly, the eastern populations have reduced indumentum as compared with the western populations. One can speculate that *O. riparia* and *O. cooperi* share a recent common ancestor. A possible scenario is that a progenitor's range became bisected, with populations that became *O. riparia* adapting and dispersing into new habitats eastward across the American Midwest and populations now referable to *O. cooperi* attaining a distribution in the southwestern U.S. and adjacent Mexico. If this is the case, *O. riparia* adapted quickly to annual hosts and a late summer to early fall flowering period, in contrast with the shrubby hosts and late winter to early spring flowering period of *O. cooperi*. Of this character set, *O. ludoviciana* shares only the semi-arid habitat and perennial hosts with *O. cooperi*, although the host taxa of *O. ludoviciana* often are herbaceous.

Orobanche riparia L.T. Collins, sp. nov. (**Fig. 1**). TYPE: UNITED STATES: INDIANA: Gibson Co.: common on bank of slough, ca. 2.5 mi N of Griffin, 16 Aug 1931, Deam 50941 (HOLOTYPE: IND; ISOTYPES: A, F, GH, IND, MINN, WIS).

Ab *O. ludoviciana* differt lobis corollae apice acutis, puberulis vel pubescentibus, tubo horizontali, constricto flexoque super ovarium, inflorescentia laxe racemosa. Ab *O. cooperi* differt corolla 15–22 mm longa, lobis corollae apice nec apiculatis nec reflexis, inflorescentia pallide purpurea.

Annual root parasite, lacking chlorophyll. Coralloid roots few, rudimentary, stout, fleshy, usually forming a single host attachment. Stem stout or slender, fleshy, 5–35 cm long, mostly subterranean, solitary or clustered, unbranched or more commonly branched from near base with a few to rarely numerous branches, each bearing a terminal inflorescence; stem base irregularly enlarged or not, 5–20 mm in diameter; glabrous, creamy white, yellow, or tan, drying ferruginous, dark brown, or black. Leaves reduced to scales, 7–10 mm long, cauline, spirally alternate, appressed, broadly ovate to ovate triangular, becoming narrower distally. Inflorescence an open spike-like raceme, glandular pubescent; bracts mostly ca. 1 cm long, the distal ones shortened, narrowly oblong-lanceolate, acute at the tip, pale lavender to dark purple. Flowers sessile or the proximal ones on short pedicels, evenly and spirally inserted on the axis, subtended by 2 small, linear-subulate bracteoles; calyces 7–11(–13) mm long, purple, deeply 5-lobed, the lobes lance-linear to linear-subulate, about equal in length, densely glandular pubescent; corollas (13–)15–22 mm long, constricted above the ovary, strongly curved at the constriction, the tube nearly horizontal, exterior surface glandular puberulent or pubescent, persistent, the tube narrow or slightly flared distally, cream-white sometimes tinted with purple, the throat with yellow palatal folds, glabrous or pubescent on folds and in grooves with eglandular trichomes; upper lip ca. 5 mm long, erect, divided about half its length, the 2 lobes triangular-acute, lavender or purple, puberulent or densely pubescent with eglandular trichomes; lower lip 3–4 mm long, divided to its base into 3 linear lobes with an acute apex, ca. 1 mm wide, pubescent with eglandular trichomes, pale, often with 1–3 purple veins. Stamens 4, inserted on the corolla tube at its constriction, generally glabrous

or with a few scattered hairs, anthers ca. 1 mm long, white, glabrous or sparsely pubescent, equalling or shorter than style. Ovary somewhat asymmetrically ovoid, 2-carpellate, nectary not evident; placentation parietal, with 4 lateral placentae; style filiform, equaling the corolla tube or shorter, stigma peltate, discoid-crateriform or rarely somewhat 2-parted. Fruits 2-valved capsules, 0.7–1 cm long; seeds numerous, 0.3–0.5 mm long, ovoid to broadly ellipsoid, reticulate-pitted, light tan to dark brown. $2n = 48$ (Collins 1973). Flowering mid-August to early October.

The species ranges (Fig. 2) from the Potomac and Shenandoah River valleys of Virginia to southern Ohio and Indiana along the Ohio River to Central Illinois along the Wabash and Sangamon Rivers, to the Meramec River in eastern Missouri (near St. Louis), southward to a tributary of the Mississippi River in western Tennessee, and westward along the Platte River in Nebraska and Eastern Colorado. Some apparently isolated populations occur in the Kansas, Oklahoma, Texas, and New Mexico along the Canadian, Cimarron, and Rio Grande rivers and their tributaries. Only historical collections are currently known from the District of Columbia, Virginia, and West Virginia. The species is found entirely on mixed sand and silt deposits on stream banks of eastern rivers or on sandbars or sandy banks of western rivers. Hosts are *Ambrosia trifida* and *Xanthium strumarium*, and occasionally *Ambrosia artemisiifolia* and *Dicoria canescens*. Rarely reported alternate hosts are *Nicotiana tabacum* L. and *N. glauca* Graham.

Representative specimens: **UNITED STATES. COLORADO: Crowley Co.:** cultivated field near Ordway, 22 Jul 1948, *Wilchusen s.n.* (CS). **Jackson Co.:** N sandhills E of Cowdry, 1 Oct 1982, *Wilken 13922* (CS). **Logan Co.:** cultivated field [along Platte River] near Sterling, *anonymous*, 8 Sep 1965 (CS). **Prowers Co.:** sandy bed of Butte Creek, 6 mi E of Two Buttes Peak, 24 Aug 1964, *Martin s.n.* (COLO, CS). **Weld Co.:** sandhills 3 mi NE of Roggen, 1 Sep 1972, *Maslin s.n.* (COLO, CS). **DISTRICT OF COLUMBIA:** E end of New Long Bridge, 2 Sep 1905, *Ward s.n.* (US). **ILLINOIS: Cumberland Co.:** banks of Embarras River, 2 mi E of Greenup, 18 Sep 1980, *Collins 1618* (MO). **Mason Co.:** bank of Salt Creek and edge of cornfield, 5 mi N of Greenview, 15 Sep 1980, *Collins 1615* (MO). **Menard Co.:** bottoms, Athens, 1860, 1861, 1866, 1867, *E. Hall s.n.* (F, GH, IL, MO, POM, WIS). **Wabash Co.:** S of Mt. Carmel along banks of Wabash River and Greathouse Creek, 18 Sep 1980, *Collins 1619* (MO). **INDIANA: Harrison Co.:** W of landing at Mauckport, 25 Aug 1945, *Deam 63566* (IND). **Jefferson Co.:** tobacco field 0.5 mi E of Brooksbury, 15 Sep 1935, *Banta s.n.* (IND). **Knox Co.:** along ditch 2 mi N of Decker, 9 Oct 1938, *Deam 59255* (IND). **Posey Co.:** E bank of Wabash River at New Harmony, 28 Aug 1971, *Collins 1555* (MO, WIS). **Sullivan Co.:** roadside S of Busseron Creek, 6.5 mi SW of Carlisle, 1 Sep 1939, *Deam 59424* (IND). **Vandenberg Co.:** river slough, 17 Oct 1941 *Zeiner s.n.* (IND). **Warrick Co.:** banks of Ohio River at Newburg, 28 Aug 1971, *Collins 1543* (UWM). **KANSAS: Allen Co.:** Iola, Sep 1925, *anonymous* (KSC). **Greenwood Co.:** potato patch near Eureka, 24 Sep 1935, *Farmer s.n.* (KS). **Morton Co.:** Cimarron River bed N of Wilburton, Aug 1929, *Gates 16205* (F, KSC, MO). **KENTUCKY: Pendleton Co.:** Ohio River bank at Ivor, 27 Nov 1942, *Chicoine 4745* (MO, US). **MISSOURI: St. Louis Co.:** exposed gravel bar on S bank of Meramec River, 2 mi N of Crescent, 1 Sep 1991, *Yatskievych & Colwell 91-195* (MO). **NEBRASKA: Buffalo Co.:** sandbar in Platte River, 2 mi S of Odessa, 8 Oct 1999, *Collins 1620* (MO, WTU). **Cass Co.:** sandbar in Platte River, 2 mi NE of Louisville, 15 Sep 1934, *Morrison 1342* (NEB). **Dawson Co.:** sandbar in Platte River, S of Lexington, 8 Oct 1999, *Collins 1621* (MO). **Kearney Co.:** sandbars of Platte River, Minden, 15 Sep 1922, *Hapeman s.n.* (PH, POM/RSA, WTU). **Lincoln Co.:** sandbar in Platte River, Sutherland, 13 Aug 1936, *anonymous* (NEB). **Merrick Co.:** sandbar in Platte River, near Central City, 22 Aug 1938, *I. Mueller s.n.* (NEB). **NEW MEXICO: Doña Ana Co.:** sand, Mesilla Valley, 25 Aug 1906, *Wooten & Stanley s.n.* (US). **Sandoval Co.:** sandy soil, Arroyo Chico, 22 Sep 1973, *Bohrer 1758* (ARIZ). **San Juan Co.:** low sand dunes on Chaco River, 30 m S of Farmington, pipeline right-of-way on BIA Road 2, 4 Sep 2007, *Collins & Heil 2032* (MO). **Socorro Co.:** sand along Rio Grande, San Marcial, 1 Aug 1897, *Herrick 825* (US). **Union Co.:** idle field, 17.5 mi SW of Clayton, 1 Sep 1936, *Cogdell 125* (GH). **OHIO: Clermont Co.:** 0.5 mi E of Chilo, 20 Oct 1949, *Bartley s.n.* (OS, US). **Hamilton Co.:** mouth of little Miami River, 25 Sep 1934, *Haller s.n.* (US). **Scioto Co.:** Nile Township along Ohio River, 29 Aug 1949, *Roth s.n.* (GH). **OKLAHOMA: Cleveland Co.:** sand in bed of Canadian River, 10 mi NW of Norman, 8 Sep 1946, *Goodman 4078* (MO). **TENNESSEE: Lauderdale Co.:** along roadway at mouth of Lower Forked Deer Creek, ca. 2 m NE of Ashport, 16 Oct 1972, *Piehl s.n.* (TENN). **TEXAS: Brewster Co.:** Boquillas Canyon, Chisos Mts., sand near Rio Grande River bank, 5 Aug 1937, *Warnock 838* (ARIZ, TEX, US). **Dallam Co.:** sandy soil, Rita Blanca Creek N of Dalhart, Aug 1949, *York & Rogers 233* (OSU, TTC). **El Paso Co.:** vicinity of El Paso, 1911, *Stearns 40* (MO, US). **Hartley Co.:** deep sand on creek bank, Punta del Agua Creek 30 mi SW of Dalhart, 26 Sep 1965, *Collins 821* (OSU, TTC). **Wheeler Co.:** 5 mi S & 7 mi E of Miami, Jul 1967, *Baggerman s.n.* (TTC, WIS, UWM). **VIRGINIA: Campbell Co.:** 8 mi from Lynchburg, 13 Oct 1933, *Freer s.n.* (US). **Page Co.:** banks of Shenandoah River, Luray, 22 Aug 1912, *Holtzman s.n.* (US). **Warren Co.:** sandy field, Front Royal, 18 Sep 1897, *Miller s.n.* (US). **WEST VIRGINIA: Summers Co.:** New River, above Shanklin's Ferry, 23 Aug 1946, *McNeill s.n.* (WVA).

Eastern and western populations have an apparent disjunction in distribution between eastern Missouri and east central Nebraska, a distance of ca. 650 km. A full list of specimens examined is available upon request to the authors. It is uncertain whether this is a true disjunction or simply the lack of intensive field work in this region to locate obscure populations (many botanists avoid botanizing in the midst of dense

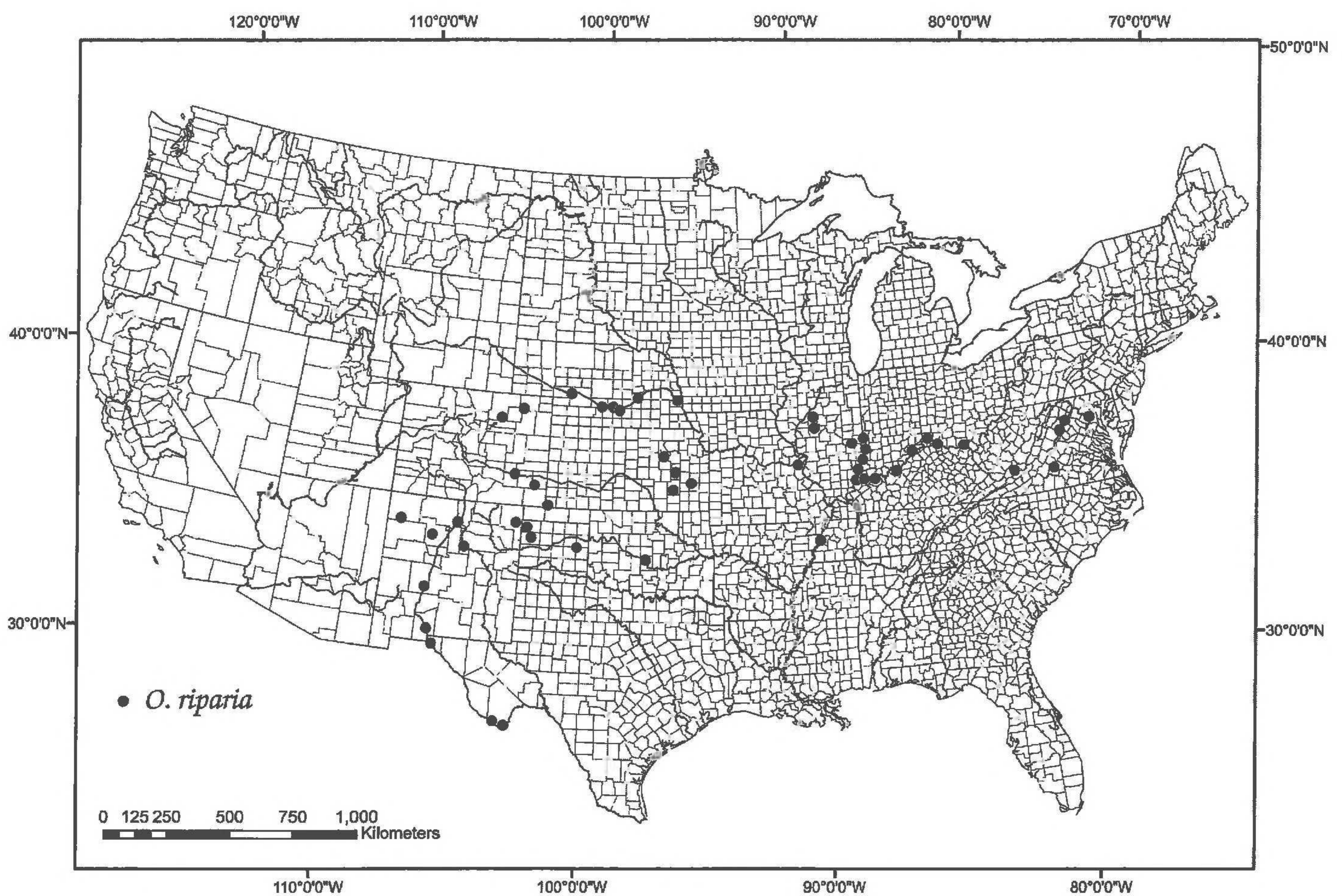


FIG. 2. Distribution of *Orobanche riparia*.

stands of ragweed and cockleburs during allergy season). The eastern and western populations of *O. riparia* exhibit slightly different morphologies. Plants of the eastern populations (including the Missouri plants) are generally pallid with very pale lavender or purple pigmentation in the corollas. Pubescence is reduced and sometimes almost absent, especially on the corolla lobes. The primary host is *Ambrosia trifida*. The habitat of these populations is floodplains with mixed sand and heavy silty loam soils of the midwestern rivers cited above.

The western populations (west of eastern Missouri) have more deeply purple-tinted corolla lobes, calyx lobes, and floral bracts. The upper stems, where exposed to sunlight, may be infused with a rosy purple. Pubescence is rather dense on the inflorescence, corolla lobes, and palatal folds. The primary host is *Xanthium strumarium*. Populations of this variant are concentrated along sand bars of the Platte River in Nebraska, with a few records of populations widely scattered in Kansas, Oklahoma, Texas, Colorado, and New Mexico. Specimens of this species collected along the Rio Grande River from central New Mexico to the Big Bend of Texas have proven problematic for identification throughout the study of Section *Nothaphyllon*. Only recently, when they were compared with the Nebraska plants, did it become apparent that they represent populations of *O. riparia*.

It is tempting to name these two variants formally as subspecies within *O. riparia*. However, the life history and morphological distinctions are not sufficient to warrant taxonomic status at this time. This problem requires more intensive study of both morphological and genetic variation within and between populations before a conclusion can be reached as to the merits of segregating infrataxa within *O. riparia*.

Host information for *Orobanche* is generally difficult to assess from herbarium labels. Collectors sometimes list as a host any adjacent plant without confirming a physical connection or list no host at all. However, host data for *O. riparia* reported here have been observed by all three authors. Only two non-Asteraceous

host reports have been confirmed. Some populations in southern Ohio occasionally parasitize cultivated tobacco (*Nicotiana tabacum*). Likewise, some populations along the Rio Grande in western Texas have been reported on the weedy, introduced *N. glauca* (the only perennial host with which the species has been associated). It is not possible at this time to judge the significance of these exceptions, if any. Anecdotal evidence suggests that other species of *Orobanche* sometimes utilize anomalous alternate hosts at the margins of their ranges.

The populations east of the Appalachian Mountains are of particular interest because they represent the extreme eastern portion of the range and may possibly be extirpated. Virginia records are represented by four herbarium specimens from four counties (on the James, Shenandoah and Potomac rivers). The most recent collection we have seen was made in 1933. A single specimen was seen from the New River, Summers County, West Virginia. The present study could not confirm extant populations in the District of Columbia, Virginia, or West Virginia. The species seems reasonably secure elsewhere in its range, although current herbarium vouchers document a highly fragmented range. For example, the single Tennessee record represents a southward disjunction of ca. 325 km from the St. Louis County, Missouri station. However, field experience of the authors suggests that this species is probably more common than the herbarium records indicate. The senior author discovered several previously unreported populations in Nebraska, Illinois, and Indiana. Additionally, a few populations were observed in Illinois, Ohio, and Texas that were located on minor tributaries (creeks) of the major river systems. Some of the historical populations were determined to be extant. Thus, it is likely that concentrated field work will reveal additional populations of *O. riparia*. The status of the historical populations in the District of Columbia, Virginia, and West Virginia especially needs to be updated by further field work.

The habitat of *O. riparia* is disturbed annually by natural events and human activity. Although it is widely distributed, populations seem to be locally isolated and therefore fragile. The senior author has observed the obliteration of a large population in Posey County, Indiana, as a result of riverbank development. Because of its unique distribution of widely separated populations in regularly disturbed habitats, the species is likely to be threatened on a local or state basis.

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